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Comparative Hedonics of Taste

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Primary knowledge of hedonics comes from introspection. The next best evidence is a verbal report: unless one believes another a liar, it is reasonable to assume that if a taste is described as pleasant, it is indeed pleasant. Comparative studies of hedonics, however, do not have available either of these sources of evidence.

The argument for the existence of hedonics in nonhuman animals is fundamentally that of homology. To the extent that other species are similar to humans they must experience similar feelings including pleasure associated with similar sensory stimulation. This argument is surely generally accepted. However, the species specificity of stimuli that determine hedonic experiences makes it difficult to generalize, even within the primates.

Two sources of indirect evidence are used to inform the argument for non-human hedonics. The first is behavioral, examples of which form the body of this chapter. The second is anatomical about which little will be said. Central nervous system structures, which in humans (*Homo sapiens*) are involved in the sensations of pleasure, are activated during certain types of sensory stimulation in nonhuman animals. Recently, there has been considerable interest in the possibility that an endogenous opioid system may modulate some aspects of the pleasure associated with sensory stimulation (Reid, 1985).

OVERVIEW OF THIS CHAPTER

Following a brief discussion of some of the issues involved in comparative chemosensory hedonics, studies of mammals and birds, the authors' respective

areas of expertise, are considered. Taste, which is emphasized, is the sensory stimulation detected by taste receptors and transmitted by the 7th, 9th, and 10th cranial nerves. The emphasis is on ingestion and the goal is not to be encyclopedic, but to consider species differences and similarities and how they may reflect ecological factors.

Comparative Hedonics: Behavioral Evidence

If, in an appropriate free choice test, an animal elects to consume one item in preference to another this is proof that it can discriminate between the two items. However, it is also generally assumed that this is evidence that the animal likes the chosen item. This is logically incorrect, as has been noted by Rozin (1979), who argued that only mimetic expression can be taken as evidence for hedonic experience in nonhuman animals. For example, an item could be preferentially selected because it is believed to be beneficial in spite of it providing unpleasant sensory experience (see Booth, 1987, who disputes this point). This distinction may be valid only in verbal humans however (Beauchamp & Cowart, 1987).

In a series of studies, Grill and colleagues (e.g., Berridge, Flynn, Schulkin, & Grill, 1984; Grill & Bernstein, 1988; Grill & Norgren, 1978; Grill & Schulkin & Flynn, 1986) have demonstrated mimetic responses to tastes in rats (*Rattus norvegicus*). Substances rats find highly palatable in acceptance tests (e.g., sweet solutions, very salty solutions when sodium deficient) elicit facial expressions indicative of acceptance whereas unpalatable tastes (e.g., bitter substances, very salty solutions to nondeficient rats), elicit expressions and behaviors of rejection. Generally speaking, acceptance studies and mimetic evaluation appear to be in accord in rats (although perhaps not in human infants; Cowart, 1981), lending some confidence to the assignment of the categories of pleasant/unpleasant to the results of preference or acceptance tests.

Although it is likely that mimetic responses would be evident in many other mammals were they to be carefully studied, birds may generally not express them. The absence of lips and the presence of a hard elongated beak limits the repertoire of facial expressions shown to oral stimulation (Gentle & Harkin, 1979). While chickens (*Gallus domesticus*) show a characteristic response to aversive oral stimulation typified by persistent tongue and beak movements, head shaking and beak wiping behavior (Gentle, 1973, 1976, 1978), no analogous repertoire has been observed in response to preferred stimuli, and no data have been collected with species other than domestic fowl.

Factors Determining Acceptance/Rejection

As in many facets of animal behavior, the interaction of innate and acquired information must be evaluated. When discussing comparative hedonics, it is assumed that species differences in sensory response somehow reflect species

differences in ecological niche. This in turn would be related, for the sense of taste, to food habits. Presumably, differences in sensory systems which permit differences in hedonic sensory experience characterize species with different niches. Hence, an unlearned component to taste hedonics should be widespread. Such is the case.

However, in highly developed forms such as birds and mammals, learning and social factors probably play a prominent interactive role. Aversions to foods may be mediated by conditioned responses (Rozin, 1976; Jacobs, Beauchamp, & Kare, 1978). Evidence for early imprinting-like attachments to odors (e.g., Leon et al., 1987) suggests that positive hedonic responses to chemosensory stimuli may also derive from individual experience, a conclusion consistent with studies of conditioned flavor preferences (e.g., Boakes & Lubart, 1988; Capaldi, Campbell, Sheffer, & Bradford, 1987; Gibson & Booth, 1986; Mehiel & Bolles, 1988; Zellner, Rozin, Aron, & Kulish, 1983). Characteristic species differences could arise from common individual experience as well as common ancestry.

Many avian species feed more efficiently when in flocks (e.g., Feare, 1984). This and other observations support the conclusion that social context may be of greater importance than physical characteristics of the food in some situations. In the laboratory, satiated red-winged blackbirds will consume food at the same rate as deprived conspecifics with whom they are in visual contact (Mason & Reidinger, 1981). Red-wings also prefer novel foods that they have seen presented to demonstrator birds (Mason & Reidinger, 1981). Social facilitation, mediated in part by chemosensation, probably plays a major role in mammalian food selection as well (see below).

Taste and Smell: A Comparison with Respect to Nutrient Intake

In contrast to the sense of taste, smell information in mammals and birds follows a path from olfactory receptors in the airway via cranial nerve I to the olfactory bulbs and thence to a variety of limbic and other CNS structures. The olfactory system serves at least two general functions in mammals and perhaps in birds, social (e.g., sex, aggression; other nasal chemosensory organs such as the vomeronasal system are also involved) and nutritive. In contrast, there is no evidence that taste plays any role other than in regulating nutrient intake and utilization. Because taste seems to have this dedicated function, it is reasonable to suppose a primary role in food acceptance. In fact, it has been argued (e.g., Ikeda, 1909; Jacobs et al., 1978; McBurney & Gent, 1979) that taste preferences and presumably taste hedonics evolved to insure adequate consumption of nutrients (calories in particular) and avoidance of poisons (often substances humans label as bitter). Under this argument, the olfactory system would play a more indirect and subtle role in modulating intake/rejection of foods. There is an apparent simplicity to the taste system, dividing as it does into a relatively few

"basic" categories (for discussion see McBurney & Gent, 1979; Erickson & Corey, 1980). In contrast, olfaction has no agreed-upon method of categorizing sensations arising from stimulation and it is often assumed that there are many, perhaps an almost infinite number, of qualitatively distinct odors that defy easy classification. This difference in the way stimuli can be categorized in the two chemosensory systems is suggestive of their functional differences. Taste is primitive, often with innately determined hedonic attributes whereas olfaction, at least in so far as food is concerned, may be more plastic, more complex, and more subtle. Animals will work to obtain tastes; in contrast, it has been difficult, although not impossible, to use odors as rewards in learning studies (Long & Tapp, 1967). In fact, while there are a number of publications emphasizing species comparisons of taste (e.g., Bell, 1959; Kare & Beauchamp, 1984), we are aware of no such enterprises for olfaction. It is these considerations that have led us to place our major emphasis on comparative hedonics of taste and to restrict our discussion of olfaction to the last section of this chapter.

TASTE

Substantial species differences in taste preferences and patterns of taste sensitivity exist. Although it is likely that these differences are generally a function of the ecological (food) niche of the different species, this hypothesis is often difficult to verify. Generally speaking, taste seems to be more highly developed in mammals than in birds.

In the following sections, examples are selected that illustrate the presumed fit between taste preference, usually revealed as responses to model aqueous solutions, and presumed food habits. As a matter of organization, this topic is divided by human taste quality; as will be evident, there are substantial problems with this approach.

Sweet Perception

While sugars (and other substances such as amino acids) described by humans as sweet are highly preferred by many species, this preference is not universal nor does it extend to all sweeteners. For example, with the exception of saccharin, most noncarbohydrate sweeteners are not preferred and are often rejected by other species tested (Jackinovich & Sugarman, 1988). An overview of species differences in sweet recognition is presented by Kare and Beauchamp (1984) and is not repeated in detail here.

Some broad differences in response to carbohydrate sweeteners among mammalian species are illustrated in Table 9.1. Cats (*Felis catus*), which are strict carnivores, appear remarkably unresponsive to carbohydrate sweeteners whereas rats and guinea pigs (*Cavia porcellus*), examples of omnivores and herbivores,

TABLE 9.1
Summary of Response of Several Species of Mammals of Aqueous Solutions of
Prototypical Taste Substances*

	<i>Species</i>					
	<i>Rat</i>		<i>Guinea Pig</i>		<i>Cat</i>	
	<i>Wild</i>	<i>Laboratory</i>	<i>Wild</i>	<i>Domestic</i>	<i>Panthera sp.</i>	<i>Felis cattus</i>
<u>Sweet Stimuli</u>						
glucose/sucrose	+	+	+	+	0	0
saccharin		+	+	+		-
L-alanine						0
<u>Salty Stimulus</u>						
NaCl	+	+	+	+		+?0
<u>Sour Stimulus</u>						
citric acid				-		-
<u>Bitter Stimuli</u>						
quinine sulfate		-		0		-
quinine						
hydrochloride		-		-		-
sucrose						
octaacetate		-		-		0

+ indicates taste solution preferred to water at at least some concentrations; rejection may occur at high concentrations;

- indicates that rejection is the prominent response; at no concentration was preference evident;

0 indicates indifference (relative to water) at all or nearly all low to moderate concentrations tested; at high concentrations, rejection may occur.

* Adapted from Jacobs, Beauchamp, and Kare (1978).

respectively, avidly consume some sweet substances. Although there is some evidence for carbohydrate preference in cats under very special circumstances (Bartoshuk, Harned, & Parks, 1971; Frings, 1951), the consensus is that cats either lack or have a very poorly developed sweet taste system (Beauchamp, Maller, & Rogers, 1977). However, Boudreau (e.g., 1986) has noted that several of the amino acids to which cats are sensitive are ones humans find sweet; perhaps the cat experiences the sensation of sweet but it occurs in response to amino acids rather than to carbohydrates.

Unfortunately, only cats (domestic and *Panthera* species), among mammalian carnivores have been rigorously investigated for carbohydrate sweet responsiveness. It is unconvincing to use the example of the cat as proof that carnivorous mammals in general lack sweet perception and preference and it would be of considerable value to examine other carnivores. Particularly attractive in

this regard are mustilids which include species that are almost strictly meat-eating (e.g., weasels (*Mustela frenata*)), as well as others that are more omnivorous (e.g., skunks (*Mephitis mephitis*)). A comparative study of sweet responsiveness among this group could be most informative.

A further comparative issue needs emphasis when discussing the apparent absence of sweet carbohydrate perception and preference in cats. There is no such thing as *the* cat or *the* dog or *the* rat. Substantial difference among populations and individuals of the same species exist, as is discussed shortly, making it often important to limit generalization (cf. Rowland & Fregley, 1989). Furthermore, most studies of taste are carried out on adult animals with developmental work often focusing on issues of when adult-like responsiveness is first evident (e.g., Hill, 1987; Mistretta & Bradley, 1983). It is conceivable, however, that different sensory capacities and preferences may characterize different developmental stages. For example, for humans it is known that children's sweet preferences are greater than those of adults (Beauchamp & Cowart, 1987; Desor & Beauchamp, 1987), although the physiological basis for this difference remains debatable (Booth, 1987). For cats, it is possible that kittens may differ from adult cats in having a functional sweet preference system, perhaps related to the nursing period. Pfaffmann (1955) reported neurophysiological responses to sucrose in one kitten but the generality of this observation is not known.

It has been argued that the wide-spread existence of a sweet carbohydrate preference in most herbivorous and omnivorous mammals tested reflects a calorie-recognition mechanism (e.g., Jacobs et al., 1978). Apparent species differences in whether sugars are preferred and in which sugars are most preferred (see Kare & Beauchamp, 1984, for examples), are, however, difficult to explain under this hypothesis. This is particularly true for avian species where the pattern of species differences is not easily interpretable.

Nectar-feeding species select flowers with high levels of sucrose, glucose, and fructose (Percival, 1961). Likewise, sugars are preferred by Bobwhite Quail (*Colinus virginianus*), Japanese Quail (*C. japonica*) (Hanrum, 1953; Brindley, 1965; Brindley & Prior, 1968; Harriman & Milner, 1969), Great Tits (*Parus major*) (Warren & Vince, 1963), Rock Doves (*Columba livia*) (Duncan, 1960), Chickens (*Gallus gallus*) (Gunther & Wagner, 1971; Gentle, 1972, 1975), Budgerigars (*Melopsittacus undulatus*) and other parrots, and the broadtailed hummingbird (*Selasphorus platycercus*) (Kare & Rogers, 1976). However, a number of avian species that *should* prefer sugars either reject them or are apparently insensitive to them (e.g., Kare, 1961, 1965; Kare & Mason, 1986; Kare & Medway, 1959). Omnivorous passerines (e.g., European starlings [*Sturnus vulgaris*], red-winged blackbirds [*Agelaius phoeniceus*]) reject sugar solutions in the laboratory (Rogers & Maller, 1973; Espaillet & Mason, 1990, cf. Schuler, 1983) but select *sweet* fruits in the field (e.g., grapes, cherries; Stevens, 1985). Possibly, this rejection of simple (disaccharide) sugar solutions reflects an inability to digest them (Martinez del Rio & Stevens 1989); other factors (e.g., pH)

may control the response (Mason, unpublished observations). In addition, many of the species that exhibit preferences for sugars do so only in short-term tests (Gentle, 1975). In long-term trials, preference behaviors dissipate, and are replaced by avoidance (Gentle, 1972).

Recently, it has been argued that there are at least two separate carbohydrate-detecting system in some mammals. One might be labeled the sweet or sugar system whereas the second might be termed a polysaccharide-detecting system. The two systems are presumably mediated by different receptors (Sclafani, 1987). Evidence in favor of such a dichotomy comes mainly from behavioral studies in rats (Sclafani, 1987) although studies in other species have been reported. Among rodents, gerbils (*Meriones unguiculatus*), hamsters (*Mesocricetus auratus*) and spiny mice (*Acomys cahirinus*), all appeared to possess a polysaccharide as well as a sugar system (Feigin, Scalafani, & Sunday, 1987). In contrast to these rodents, cats are, as would be predicted, indifferent to both sugars and polysaccharides (Harrison, Castonguay, Scalafani, & Rogers, 1986, cited in Sclafani, 1987). Amongst primates, humans (Feigin et al., 1987) and squirrel monkeys (*Saimiri sciureus*) appear to lack the polysaccharide system while bonnet macaques (*Macaca radiata*) apparently possess one (Sunderland & Sclafani, 1988). While Sunderland and Sclafani argue that these differences between nonhuman primates are consistent with their natural food preferences, this is speculative; other primate species need to be evaluated to test the fit between dietary behavior and presence or absence of the hypothesized polysaccharide system.

Bitter Perception

As a companion hypothesis to the sweet-calorie association, it has often been suggested that bitter perception exists to protect animals from ingesting poisons, mainly alkaloids, and to protect plants from being eaten. In general, bitter substances are offensive to many species, although as with sweeteners, there are marked interspecific differences.

Quinine hydrochloride is bitter to humans, and rejected by many species; however, the rejection threshold exhibits marked interspecific variation as shown by comparing studies of cats, rats, and guinea pigs (Tables 9.1 and 9.2). While methodological differences could account for some of this variation, Jacobs et al. (1978) suggested that the importance of bitter tastes, and thus sensitivity of the bitter system may depend upon the feeding ecology of the species in question. In particular, the guinea pig is a strict herbivore and as such, is confronted with the problem of consuming sufficient calories from plants, most of which taste bitter to humans. Given this problem, if guinea pigs had a sensitive bitter-rejection mechanism they would have substantial difficulty in finding acceptable foods.

Even more extreme are species differences among birds. Quinine hydrochloride or sulfate are rejected by some species of birds (e.g., pigeons [Duncan,

TABLE 9.2
Relative Sensitivity (in Preference Tests) of Three Domestic Species to a Bitter
Substance, Quinine Hydrochloride

CAT RAT GUINEA PIG					
-6	-5	-4	-3	-2	-1
QHCI CONCENTRATION (10 ^x)					

Note. Rats and, particularly, cats are much more sensitive (several orders of magnitude) to QHCI than guinea pigs. All rejection levels determined in two-choice preference tests with aqueous solutions. For references, see Jacobs, Beauchamp, and Kare (1973).

1960], ducks and chickens [Engelmann, 1934]), and for a few, such as the Black-capped Chickadee (*Parus atricapillus*), these compounds are toxic. However, bread mixed with quinine is readily eaten by some parrots (*Amazona* spp.), and grain dipped in picric acid is readily consumed by seed eaters and titmice (*Parus* spp.) (Heinroth, 1938). Both denatonium saccharide and denatonium benzoate (bitrex) are extremely bitter to humans, but readily accepted by red-winged blackbirds (Mason, 1987). Likewise, sucrose octaacetate at a concentration bitter to humans is readily accepted by the herring gull and the chicken, but rejected by Bobwhite and Japanese Quail (Brindley, 1965). At least for this compound, there are indications of ontogenetic changes in sensitivity. Bobwhite Quail do not respond to sucrose octaacetate as young birds, but gradually develop the ability to detect and avoid it (Cane & Vince, 1968).

If some herbivorous birds and mammals (see Jacobs et al., 1973) have a blunted bitter-rejection system, what is to prevent them from ingesting excessive poisonous compounds? While there apparently is a rough correlation between bitterness and toxicity (Scott & Mark, 1987) this correlation is not perfect. It is suggested that another mechanism to avoid toxins is the formation of conditioned aversions to other flavor components of a toxic plant. If there is no innate bitter-alkaloid-based rejection of plants, the animal is free to sample and, in effect, meter the intake of toxic plants at an acceptable level.

Alternatively, or in addition, herbivorous animals could develop detoxifying mechanisms; this is a common insect strategy. It is probably the plant-insect interactions that have led the way to the bitter-rejection system in vertebrates. In one interesting example of this strategy, Glendinning (1988) has studied mouse (*Peromyscus melanotis*, *P. aztecus hylocetes*, *Reithrodontomys sumichrasti* and *Microtus mexicanus*) predation on monarch butterflies (*Danaus plexippus*) at the latters' wintering grounds in Mexico. Of the four species of mice present in the area, only one (*P. melanotis*) makes extensive use of the vast protein store potentially available from these butterflies. Since the butterflies contain toxic

cardiac glycosides that are bitter and can cause emesis (e.g., Brower, 1969), how is this ecological challenge met by the mouse species? Experimental studies (Glendinning, 1988) demonstrated that the one species known to prey upon monarchs in the field was the only one which (1) extensively ate monarchs in test situations; (2) gained weight; and (3) selectively ate those parts which were least toxic (for a similar observation with guinea pigs, see Jacobs & Labows, 1979). It is suggested that the predatory species is probably less sensitive (though not completely insensitive) to the taste of cardiac glycosides, a result confirmed in formal taste studies (Glendinning, 1988), is able to withstand ingestion of relatively high levels of toxic compounds and is likely to have well developed behavioral techniques for assessing the nutritive value of food, for example, the ability to form conditioned aversions (Glendinning, 1988). Similar principles may apply in other cases. The skin of salamanders (*Amphystoma tigrinum*) contains toxins that prevent predation. The skin secretions produce primary and conditioned aversions in rats (Mason, Rabin, & Stevens, 1982), yet shrews (*Blarina brevicauda*) will eat salamanders (Brodie, Newark, & Harvey, 1979).

The marked species differences in bitter perception suggested by Glendinning's studies are further complicated by the evidence for different types of bitter receptor mechanisms. It is well known that for humans and some other species, an individual's sensitivity to the bitter compound phenylthiocarbamide (PTC) is not strongly predictive of responsiveness to other bitter compounds such as quinine hydrochloride or sucrose octaacetate. The ability to detect PTC at low concentrations is bi- or tri-modally distributed in human populations and is under genetic control (Morton, Cantor, Corey, & Nance, 1981). To the extent that sensitivity to the other bitter substances is also under genetic control, other genes appear to be involved.

Studies of genetic control over bitter perception by inbred strains of mice (*Mus musculus*) have demonstrated the existence of several genes determining sensitivity to specific bitter substances. Lush (1981, 1982, 1984, 1986; Azen, Lush, & Taylor, 1986) postulates at least four separate genes which have been labeled *Soa*, *Qui*, *Rva* and *Cyx*, that control ability to detect specific bitter substances. The presence of these genes has been based on preference studies: Mouse strains which are indifferent to a certain chemical such as sucrose octaacetate (*Soa*) presented in a two-choice test against water are concluded to be unable to taste *Soa*. However, because preference tests cannot be used to confirm an absence of sensitivity or ability to detect, the issue remained as to whether these proposed genes were truly involved in sensitivity, perhaps indicating the presence or absence of specific receptor proteins. Recent studies of sucrose octaacetate sensitivity by inbred strains of mice in Whitney's Laboratory (e.g., Harder et al., 1984; Whitney, Harder, Gannon, & Maggio, 1989) have demonstrated that sensitivity to *Soa* is under genetic control. Furthermore, Shingai and Beidler (1985) have shown that the strain differences in behaviorally-determined sensitivity are mirrored in parallel electrophysiological differences, further sup-

porting the idea that the genes are involved in coding for receptor-associated proteins.

These studies lead to the conclusion that bitter perception is not a unitary phenomenon. This is not surprising if one believes that perception and rejection of toxic compounds is the "function" of a bitter taste system. To date, there is no agreed-upon chemical basis for bitterness and this may be because no common molecular configuration exists for this taste. Instead, as plants and perhaps insects (Brower, 1969; Yang & Kare 1968) have evolved substances that are potentially harmful to invertebrates and vertebrates alike, these organisms have evolved means to detect the substances. Specific taste mechanisms have, as a result, developed as a family of different protein-based receptors, all of which are connected to genetic rejection mechanisms and which elicit more or less common sensory experience humans label as bitter and unpleasant. Before this broad scenario is taken very seriously, however, considerably more comparative study is needed, especially studies that attempt, as in the Glendinning work, to correlate sensory capacity with natural food habits.

Salt Perception

The salty taste is probably the most specific of the classic taste qualities reflecting the need to maintain sodium balance (Dethier, 1977). As salt taste is treated in other chapters in this book as well as having been given extensive review in Denton's (1982) monumental work, only a few comparative topics are touched on here.

Two aspects of the behavioral response to salt have been investigated, responses to salt during sodium depletion (often called salt appetite) and response to salt during a period where the animal has sufficient body sodium (often called salt preference). Whereas the same sensory channel is presumably involved in both situations, the mechanisms underlying behavioral responses may be different and species difference could apply in one instance but not another.

Mechanisms of salt appetite have been studied in exquisite detail in rats and sheep (*Ovis aries*), which surprisingly exhibit marked species differences (Denton, 1982; Epstein et al., 1984; Epstein & Sakai, 1987). Particularly relevant to the topic here, depletion appears to induce a hedonic shift in response to high salt concentrations, moving them from unpleasant to pleasant as determined by rat mimetic responses (Berridge et al., 1984). Recent studies, expanding the original work by Contreras and Frank (1979) which demonstrated neurophysiological changes following sodium depletion, now suggest that the neurophysiology of salt taste response becomes more sweet-like during sodium depletion (Jacobs, Mark, & Scott, 1988). However, the interesting question of whether salt tastes sweet to a salt-depleted animal has not yet been adequately evaluated. Perhaps the connection in the literature between sweet and good is more than mere hyperbole: For taste response, the more pleasant may literally be sweeter. This is one

of the many interesting issues of sensory effects of salt depletion which could be studied best if it were possible to use modern psychological techniques to deplete human (verbal) subjects (Beauchamp, Bertino, Burke & Engelman, 1990). However, it should be pointed out that the evidence for a salt appetite following acute depletion in adult humans is not strong (Beauchamp, 1987; Beauchamp et al., 1990; Stricker & Verbalis, 1988). Species differences suggest caution in assuming that salt-depleted humans would manifest a salt appetite identical with that observed in sheep or rats. In this regard, the dog, which mainly eats meat and might not experience sodium deficiency in nature without first starving, does not appear to develop a sodium appetite following experimental depletion (Thrasher, personal communication). A chemosensory-connected mechanism to detect depletion of sodium may not exist in carnivorous animals in general (see Table 9.1).

For comparative work, the majority of studies involve salt taste perception in sodium-replete individuals. Under these physiological conditions, some mammalian species exhibit preference for hypotonic and near-isotonic salt solutions relative to water, whereas others do not (Carpenter, 1956). Rensch and Neunzig (1925) assessed sodium chloride sensitivity in 60 avian species. Variability was enormous, ranging from low thresholds for parrots (0.35%) and pigeons (0.5–0.9%) to high thresholds for gray partridge (*Perdix perdix*; 20%) and siskin (*Carduelis*) species (37%). Unlike rodents that avidly select some hypotonic concentrations of sodium chloride, many birds are indifferent up to the threshold concentration for rejection. This threshold is usually the point at which the solutions become hypertonic relative to body fluids (Bartholomew & Cade, 1958; Bartholomew & MacMillan, 1960). Not surprisingly, birds with nasal salt glands will drink seawater, but even these species avoid consumption of saltwater when opportunities arise. Both the Herring Gull (*Larus argentatus*) and the Laughing Gull (*L. atricilla*) will select pure water over salt solutions when given a choice (Harriman, 1967; Harriman & Kare, 1966). Similarly, penguins are said to prefer fresh over seawater after having been at sea for extended periods (Warham, 1971).

It is only among birds without salt glands that preferences for salt are observed. Numerous finches of the family *Carduelidae* possess notorious appetites for salt, and cross bills can be caught in traps baited with salt alone (Welty, 1975; Willoughby, 1971). Domestic fowl are rather insensitive to sodium chloride (Engelmann, 1934), although if maintained on a low sodium diet they will exhibit a specific appetite and select, in choice situations, the diet or solution that corrects the deficiency (Kare & Rogers, 1976; cf. Hughes & Wood-Gush, 1970).

At least for domestic fowl, there appear to be developmental changes in sensitivity. Engelman (1950) reported that chicks were considerably more sensitive to sodium chloride than adults, and speculated that this might reflect their inability to handle high salt concentrations (Kare & Beily, 1948). Rodents also appear to exhibit developmental changes in sensitivity to salt (Hill, 1987), and

recent evidence indicates that there may be critical times during development when the fetal rat must be exposed to salt in order for normal taste responses to emerge. In a series of electrophysiological experiments, Hill and Przekop (1988) have demonstrated that rat pups deprived of salt prior to fetal day 8, via sodium deprivation of their mothers, never develop normal salt sensitivity. These findings are especially intriguing, because the period of deprivation occurs prior to the development of receptor cells. Apparently, changes in the central nervous system are responsible for these observations.

The order of sensitivity of ionic series by birds does not appear to fit into the lyotropic or sensitivity series reported for other animals. No physical or chemical theory has been offered to explain the responses to sodium salts and chlorides, and there is considerable individual variability. Often, the distribution of thresholds is continuous with reactions among birds to a single concentration of one salt varying from preference to rejection. Chemical specificity is involved, because an individual that can taste one salt at either unusually high or low concentrations is likely to respond in an average manner to other salts. It has been possible to select and breed for taste sensitivity to a specific chemical (Kare, 1961).

The inability to predict acceptance of hypotonic saline solutions by avian species is something of an enigma. Jacobs et al. (1978) hypothesized that since free-ranging herbivores tend to experience chronic salt deficiencies (Abraham et al., 1975), then most should exhibit salt preferences, even in the absence of deficiency. This is not generally the case with mammals (Jacobs et al., 1978). Nor, as reviewed here, is it the case with herbivorous (granivorous) birds, who rarely show symptoms of sodium deficiency when kept on a low salt diet (Cade, 1964; Dawson, Shoemaker, Tordoff, & Borut, 1965). Perhaps the discrepancy between prediction and observation is more apparent than real, since for birds no careful attempt has yet been made to examine salt preferences in birds that are given maintenance diets in which sodium levels are controlled.

Does a preference for saline mean that when it occurs, animals *like* or obtain pleasure from the salty-tasting solutions? This is a question that has vexed many investigators and as yet is unresolved. Deutsch and Jones (1960) were among the first to suggest that a salt preference may represent something other than the drive for the pleasant taste of salt. Their hypothesis, put in its most simple form, was that rats consume more salt solution than water because the former is, in effect, dilute water and hence more of it is needed to reach the same hydration level. This hypothesis has aroused considerable controversy (see Denton, 1982) and it is safe to say that the issue remains unsettled. These observations have stimulated a body of work, among the most interesting is the observation that there is some difficulty in inducing rats to work to obtain presumably pleasant salt solutions (see also Mook, 1963; Myer & Van Hemel, 1969; Rabe & Corbit, 1973; Stellar, Hyman, & Samet, 1954), a great contrast with the reinforcing value of sweet stimuli.

Most comparative work has involved salt preference for saline solutions. As is the case for sucrose, there are good reasons for hypothesizing differences in salt taste as a function of the extent to which meat forms a portion of the organism's diet. Meat, in particular blood, is considerably higher in sodium than is the average plant and thus it is likely that omnivores are under considerably more sodium stress than are carnivores. Consistent with this proposal, saline preference in mammals is reported in omnivores and herbivores but generally not in carnivores (see Table 9.1; Denton, 1982). A postnatal maturation of the salt taste system observed in sheep (Mistretta & Bradley, 1983), rats (Hill, 1987), and perhaps in humans (Beauchamp, Cowart & Moran, 1986) also accords well with a hypothesis linking salt taste perception and preference to the possibility of depletion. Presumably, no depletion is possible (before frank starvation) during the nursing period. For precocial chicks, for which *excess* consumption could be a problem, a highly developed sense very early would be important (see above). As with sweet perception, a more focused comparative study of salt taste and diet would be of considerable interest.

One final observation is relevant to the issue of the pleasantness of salt to non-deprived organisms. Recent studies with rats (Beauchamp & Bertino, 1985; Bertino & Beauchamp, 1987) have been unable to demonstrate salt preference in the context of a solid food; instead salty solid foods appear to be rejected relative to the same foods without salt. Since these same rats prefer saline solution to water, the generality of the pleasantness of the salty taste is in question. Although there is little comparative work along these lines, the results of studies with baboons (Barnwell, Dollahite, & Mitchell, 1986) were also consistent with a lack of salt preference in food. In this regard, rats and baboons contrast strongly with humans where salt preferences are almost universally expressed in a food.

Sour Perception

Remarkably little informative work has been conducted on comparative aspects of sour taste perception. Most mammals and avians are sensitive to acids in solution, and exhibit avoidance of them. Rensch and Neunzig (1925) found that most of the 60 bird species they tested showed a narrow tolerance for acetic acid in solution and that rejection thresholds usually were below 1.0%. Engelmann (1934) obtained similar results, reporting that pigeons were more sensitive than either ducks (*Anas platyrhynchos*) or geese (*Anser anser*). Differential sensitivity has also been observed for passerines: starlings are more sensitive than red-winged blackbirds, though both species exhibit rejection (Espaillat & Mason, 1990; cf. Harriman, 1968). For domestic fowl, Engelmann (1950) reported that chicks are more sensitive than adults, suggesting (as for salt) that there might be ontogenetic changes in sensitivity. Analogous developmental changes may be true of European starlings (Stevens, 1985). While most species exhibit rejection of acids, there

are exceptions, and some birds exhibit preferences. Thus, Brindley and Prior (1968) reported that Bobwhite Quail prefer 0.05% HCl to water.

The ecological relevance of high sensitivity for acids coupled with low tolerance is unclear, although these characteristics may be useful in food selection (Harriman, 1968). Acids are present in many food items, notably fruits. A high sensitivity for an acidic taste in potential food items could be one clue as to its palatability. Too strong an acidic component could signal unripeness, leading to rejection (hence the low tolerance for acidic solutions). However, while there are likely species differences related to food habits, obvious hypotheses to account for those differences, such as a greater preference among frugivorous species, have not received adequate attention. Even the existence of sour as a fundamental class of taste perception is an enigma since sensitivity to acids apparently occurs at much lower levels than those which could be considered caustic or dangerous.

Other Tastes

Amino acids act as taste stimulants for most species studied. As might be expected, animals that eat foods likely to be identified by free amino acids seem more responsive to their taste. Fish, particularly catfish (*Ictalurus punctatus*), are known to be exquisitely sensitive to a variety of amino acids and this organism has recently become one of the major model species for the investigation of the biochemistry and biophysics of taste reception and transduction (see various papers in Brand, Teeter, Teeter, & Kare, 1989). It is likely that something approaching a full understanding of the biochemical mechanisms of taste will come from studies with this species. Interestingly, the catfish responds to many of the same amino acids with both its olfactory and taste systems.

The available evidence suggests that a variety of avian species are also sensitive to amino acids. Some, such as the European starling (Espaillat & Mason, unpublished observations) and bullfinch (*Pyrrhula pyrrhula*; Greig-Smith, Wilson, Blunden, & Wilson, 1983), exhibit the ability to detect L-alanine and other amino acids at concentrations below those that are generally detectable by mammals (personal observation). At least in part, high sensitivity may help explain foraging responses of these birds in the field. Possibly, the ability to detect low levels of free amino acids may aid starlings in their selection of the high protein fraction of complete diets for livestock (Feare & Wadsworth, 1981). Likewise, foraging by bullfinches on pear flower buds is positively associated with free amino acid concentrations in the buds of various pear cultivars. Suggestively, a variety of shorebirds, including Purple Sandpipers (*Calidris maritima*), Red Knots (*Calidris canutus*), Sanderlings (*Calidris alba*), and Dunlins (*Calidris alpina*), can discriminate between jars filled with sand containing "taste" and "no-taste," where *taste* is derived from worms that had lived in the sand, but had been removed before the experiment (Geritsen & Sevenster, 1985).

It would not be surprising if free amino acids in the skin mucous of the worms was the stimulus detected by the birds.

Among mammals, amino acids may be perceived as similar to other sweet, sour, salty, or bitter stimuli or they may be distinct. As noted earlier, Boudreau (e.g., 1986), has argued that some amino acid-sensitive fibers in cats are identical with sweet-sensitive fibers in other species with the exception that the former do not respond to simple carbohydrates. Similarly, Kasahara, Iwasaki, and Sato (1987) present neurophysiological and conditioned aversion data that mouse preference for D- and L-amino acids is due to their sweetness. Boudreau et al. (1985) have suggested that, relative to carnivores such as the cat and the dog, the rat is insensitive to amino acids.

Humans too tend to describe most amino acids as sweet, bitter, tasteless and less commonly sour and salty (Schiffman, Sennewald, & Gagnon, 1981). However, one qualitatively distinct experience, that labeled "umami," follows stimulation by glutamate (usually the monosodium salt, MSG) often in conjunction with the 5'-ribonucleotides, as well as other amino acids. It has been hypothesized that this flavor is indicative of protein (amino acid) sources and has evolved as a sensory signal for that nutrient in much the same way sweet perception involves calorie regulation (Ikeda, 1909). A rare synergistic interaction between MSG and the 5'-ribonucleotides has been documented (see chapters in Kawamura & Kare, 1987). Interestingly, the flavoring properties of both these substances as well as their synergistic interaction were first discovered and exploited in Japanese cuisine where foods containing MSG (seaweed) and ribonucleotides (mushrooms) were combined long before the chemical nature of the active ingredients was known.

The status of an umami taste remains somewhat controversial but there is no doubting that monosodium glutamate provides a singular sensory experience to humans. Whether such a system exists in other species is controversial (Kawamura & Kare, 1987); Boudreau finds the only similar system from a neurophysiological perspective in the lobster (*Homarus* sp.; Boudreau, 1986; Johnson, Voight, Borroni, & Atema, 1984).

OLFACTION

For many animals, palatability is a function of *flavor*, that is, both taste and volatile characteristics, rather than of taste alone. Thus, for carnivores (e.g., domestic cats) both the duration and the size of meals is increased by perfusing normally preferred meat odors (e.g., cooked rabbit) through the maintenance diet (Mugford, 1977). Even satiated animals can be induced to eat using this method. Similarly, Larue and LeMagnen (1972) report that food odors can enhance feeding by rats. But food odors alone are not the only volatiles that contribute to food selection. Endogenous cues produced by conspecifics are also important. This point is illustrated in a series of recent experiments by Galef and his

colleagues. When faced with a choice among several novel foods, naive "observer" rats choose foods eaten by "demonstrator" conspecifics with whom they previously have interacted (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984). Social transfer of diet preference is mediated in part by volatile cues (Galef & Stein, 1985).

Important volatile information could be the smell of food that a demonstrator has ingested before interacting with an observer. Alternatively, transmission might require a combination of the smell of ingested diet and some endogenous (demonstrator-derived) cue. In experiments designed to test these possibilities, Galef and Stein (1985) and Galef, Kennett, & Stein (1985) showed that the smell

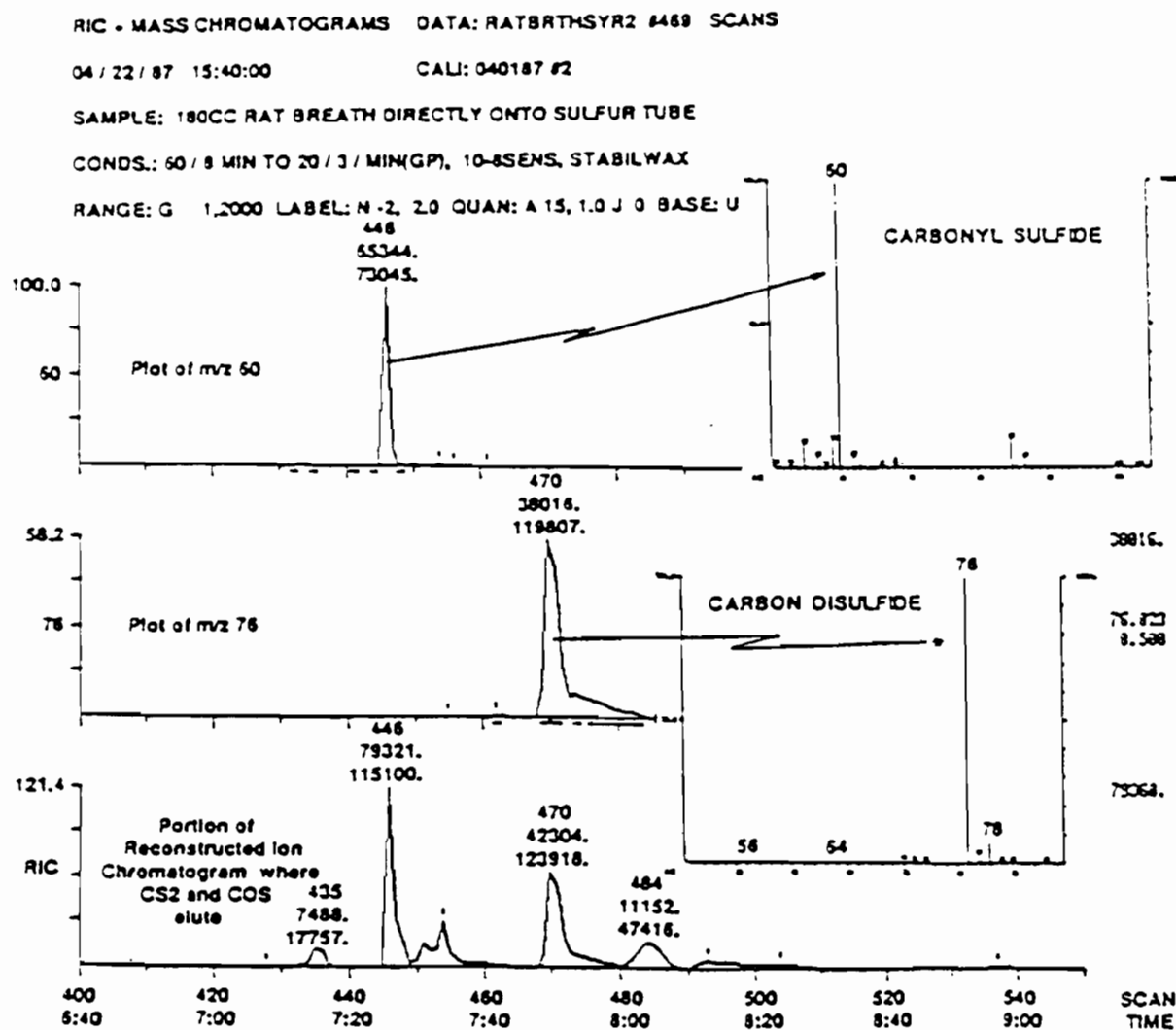


FIG. 9.1. Reconstructed ion chromatograms of rat breath showing molecular ions for COS and CS₂. The spectrum of CS₂ consists mainly of the molecular ion m/z 76, the sulphur-containing isotope ion at m/z 78, and a small fragment ion at m/z 64. The spectrum of COS consists mainly of its molecular ion at m/z 60 and an isotope at m/z 62. From Galef et al. (1988).

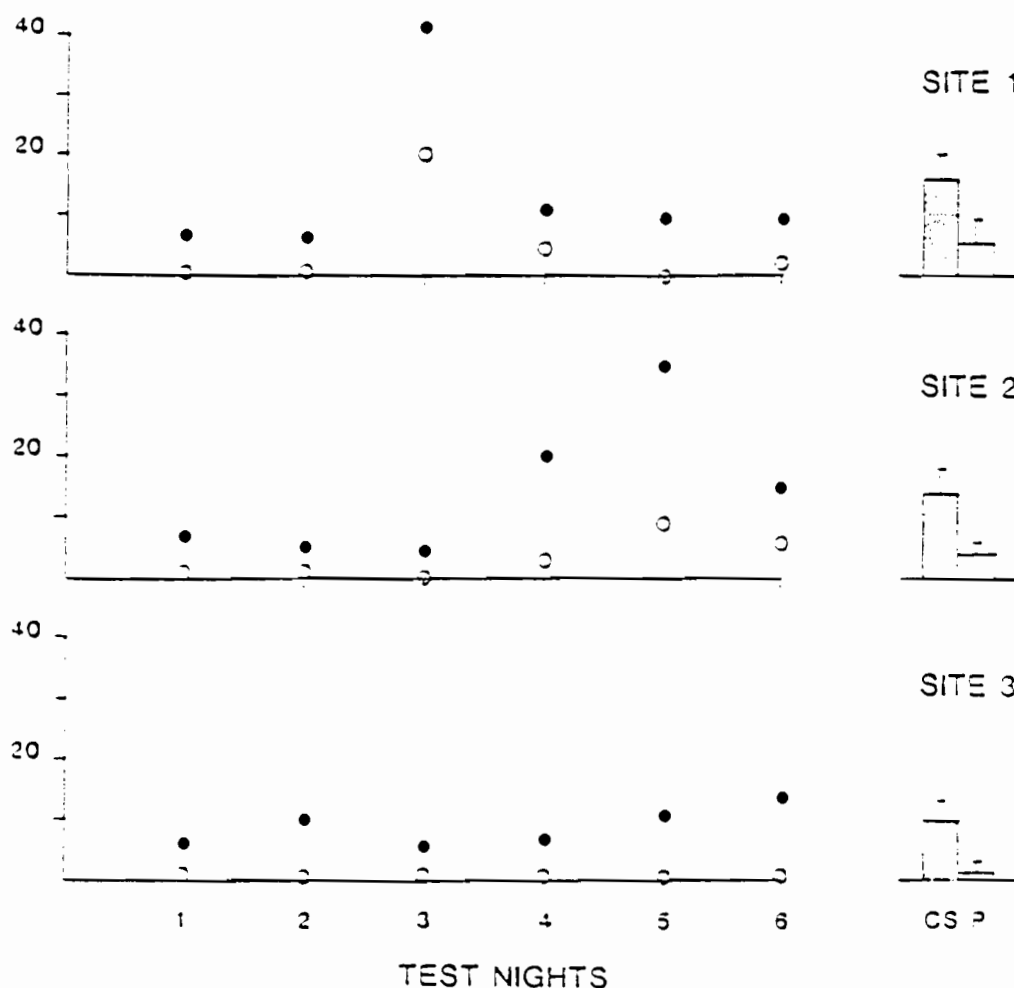


FIG. 9.2. (A) Consumption at several test sites during six nights of bait presentation. Open dots represent consumption (g) of unscented bait. Shaded dots represent consumption of CS₂-scented bait. (B) Mean consumption at each site, collapsed across tests. Open and striped bars represent consumption (g) of unscented and scented baits respectively. Capped vertical lines show the standard errors of the means. From Mason et al. (1988).

of ingested diet and demonstrator-produced volatile signals provided important information. In a series of gas chromatographic/mass spectroscopic experiments, Galef, Mason, Preti, and Bean (1988) found that carbon disulfide (CS₂) is present on the breath of rats at a concentration of about 1 ppm. (See Fig. 9.1.)

When CS₂ is associated with diet, observer rats subsequently prefer the diet (Galef et al., 1988) and only acquire conditioned taste aversions for it with difficulty. Mice show similar preferences for CS₂, and the effect is stronger for females than it is for males (Bean, Galef, & Mason, 1988). When CS₂ is paired with diet in field tests with wild Norway rats (Mason, Bean, & Galef, 1988), consumption of diet is tripled (Fig. 9.2), and neophobia is significantly reduced.

It is possible that the attractiveness of sulfur compounds is related to the feeding strategies of the animal in question. Sulfurous odors appear to attract

meat-eating species. Carbon disulfide is attractive not only to omnivores such as rats and mice, but also to primarily carnivorous species such as dogs and cats. Garlic odor (diallyl disulfide) is a flavor additive to dog foods (D. Passe, personal communication), and since successful coyote lure formulations always contain sulfurous odorants (G. Preti, unpublished), it is likely that sulfurous compounds are attractive to these canids as well.

Unlike carnivores and omnivores, there is both anecdotal information and empirical evidence that sulfur-containing compounds are repellent to herbivores. Grazing ungulates such as mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*), as well as herbivorous rodents such as mountain beaver (*Aplodontia rufa*) are repelled by Big Game Repellent (BGR) (Campbell, personal communication), a complex mixture of ingredients (including sulfurous materials). Anecdotal information suggests that BGR may be attractive to coyotes. In the laboratory, CS_2 at 1 ppm (an attractive concentration to rats and mice) is strongly avoided by herbivorous guinea pigs (Mason, unpublished observations). Interestingly, gas chromatographic analyses of guinea pig breath samples indicates that no CS_2 is present, although hydrogen sulfide may be (Preti, unpublished observations).

The omnivore-carnivore/herbivore difference may span across Classes (Aves and Mammalia) as well. Among birds there is evidence that carnivores (e.g., turkey vultures, *Cathartes aura*) not only find food on the basis of sulfur containing volatiles (Houston, 1986; Stager, 1967), but also may reject meat on the basis of sulfurous compounds from carcasses that have rotted (Houston, 1986). Conversely, herbivorous species (e.g., Canada geese, *Branta canadensis*) avoid plants such as wild onion, perhaps because these plants exude sulfur-containing odorants (such as S-propyl propane thiosulfinate).

The origins of sulfur gases on the breath of omnivorous rodents remains unclear, although most likely, these materials are a result of bacterial fermentation (R. O'Connell, personal communication). If fermentation is the source of sulfur attractants, then a variety of intriguing but unaddressed questions arise. Would mice or rats raised without gut bacteria show preferences for foods paired with CS_2 ? Could preferences be altered by manipulating the kinds of bacteria present in the gut? Could preference for sulfur compounds be induced in herbivores inoculated with appropriate bacterial strains?

CONCLUSIONS

The ecological implications of differences among individual animal strains and species in taste and smell sensitivity and preference are obvious. Differences permit several species to co-exist in the same environment by utilizing different foods. Importantly, intraspecific variability in sensitivity (i.e., individual differences) permits the development of "skill pools" (Giraldeau, 1984), which

permit individuals to survive changes in the availability of food types and to rapidly exploit newly available foods.

This generalization, however, is based on remarkably little in the way of rigorous comparative study. Attempts to characterize microadaptation of species' taste behavior and physiology to specific variation in available and exploited food sources are few. The study of monophagous animals could shed considerable light on the relationships between ecological niche and sensory worlds. In this regard, the aardwolf (*Proteles cristatus*) is almost unique (Richardson, 1987a, 1987b) as a carnivorous dog-like mammal which feeds almost exclusively on a single source, the unpalatable harvester termite (*Trinervitermes* sp.). These termites have a defensive sticky noxious terpene-based secretion and are avoided by virtually all other predators, vertebrate and invertebrate alike. In contrast, the aardwolf has evolved a series of anatomical and perhaps sensory adaptations which allow it to overcome the defense system and feed on this source exclusively so that it has been calculated (Richardson, 1987a, 1987b) that an animal consumes over 100 million termites/year. A study of this animal's taste sensitivity and preference would be fascinating and illuminating.

To return to the theme of this volume, it is assumed that sensory stimulation, in this case chemosensory experience, which though evolution has been associated with factors which benefit individual survival, has come to elicit pleasure. If this is so, the senses of taste and smell provide a forum for comparative investigation of hedonics which remains to be fully exploited.

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